



TITLE:

The neural correlates of endowment effect without economic transaction.

AUTHOR(S):

Votinov, Mikhail; Mima, Tatsuya; Aso, Toshihiko; Abe, Mitsunari; Sawamoto, Nobukatsu; Shinozaki, Jun; Fukuyama, Hidenao

CITATION:

Votinov, Mikhail ...[et al]. The neural correlates of endowment effect without economic transaction.. Neuroscience research 2010, 68(1): 59-65

ISSUE DATE:

2010-09

URL:

<http://hdl.handle.net/2433/126834>

RIGHT:

© 2010 Elsevier Ireland Ltd and the Japan Neuroscience Society; この論文は出版社版ではありません。引用の際には出版社版をご確認ご利用ください。 ; This is not the published version. Please cite only the published version.

Journal Section: Cognitive/Computational Neuroscience

Title: *The neural correlates of endowment effect without economic transaction*

Authors and author addresses: Mikhail Votinov¹, Tatsuya Mima¹, Toshihiko Aso¹, Mitsunari Abe², Nobukatsu Sawamoto¹, Jun Shinozaki³, Hidenao Fukuyama¹

Human Brain Research Center, Kyoto University Graduate School of Medicine, Shogoin, Sakyo-ku,
Kyoto 606-8507, JAPAN

² Human Cortical Physiology and Stroke Neurorehabilitation Section, National Institute of Health, 10
Center Drive MSC 1428, Bethesda, MD 20892-1428 USA

³ Department of System Neuroscience School of Medicine, Sapporo Medical University, JAPAN

Corresponding author: Hidenao Fukuyama, fukuyama@kuhp.kyoto-u.ac.jp

Human Brain Research Center, Kyoto University Graduate School of Medicine, Shogoin
Kawahara-cho54, Sakyo-ku, Kyoto 606-8507, Phone +81 (0)75 751 3603, Fax +81 (0)75 751 3202 Japan

Number of figures and tables: 5 figures

Contents of supplemental material (if applicable): none

Number of pages: 26

Number of words: Abstract – 143 words; Introduction – 447; Discussion - 1981

Keywords: loss aversion, endowment effect, reward, decision-making, fMRI, VBM, IFG, Insula

Acknowledgements: This study is partly supported by the Grants-in-Aid for Scientific Research on Priority Areas (Integrative Brain Research) for T.M. (20019023) and Strategic Research Program for Brain Sciences (SRPBS) for TM from the MEXT of Japan, and Grant-in-Aid for Scientific Research (C) 21613003 for T.M. from Japan Society for the Promotion of Science.

Abstract

People always concern about what they have and what they might lose even it is just imaginary property. According to Prospect Theory, the losses might be weighted by subjects higher than gain, which would cause the disparity between the willingness to accept (WTA) and willingness to pay (WTP) compensation in economic valuation. Using functional MRI, we investigated neural correlates of this inconsistent value estimation, known as the endowment effect, during a simple pricing task without economic transaction. Brain activation associated with this price discrepancy was observed in the right inferior frontal gyrus (IFG), where voxel-based morphometry of MRI revealed the positive correlation between gray matter concentration and WTA/WTP ratio. These findings suggest the functional relevance of IFG in WTA/WTP discrepancy for pricing without any actual gain and loss, where an integration of loss aversion-related signals from insula and expected value signals may occur.

Introduction

In everyday life, we encounter advertisements on TV saying “Try it risk free for 30 days. If you do not find it to be everything you hoped for, simply send it back to us and you will get a full refund of the purchase price.” Mail-order businesspersons know very well that this money-back guarantee strategy works well and that consumers rarely send the item back but rather prefer to keep it once they possess it. If we are Homo Economicus who can always make a rational choice, the ownership during the trial period should not make any difference in our preference (Coase 1960; Simon 1955). However, behavioral studies consistently showed that this is not the case (Brookshire and Coursey 1987; Kahneman et al. 1990; Knetsch and Sinden 1984)

This behavioral bias in decision-making has been known as the “endowment effect”(Thaler 1980). People value the item they own more than the identical item that is available for purchase in a stock of the distributor. In other word, people typically require more compensation to give up their possession than they would have been willing to pay to obtain it (Bateman et al. 2006; Horowitz and McConnell 2002; Kahneman et al. 1990; Knetsch and Sinden 1984). One possible explanation of this effect comes from the prospect theory (Kahneman et al. 1991; Kahneman and Tversky 1979; Kahneman and Tversky 1984). An individual has the tendency to weigh losses more heavily than gains of similar size, so that changes in the reference point can alter choices (Ariely et al. 2005; Kahneman and Tversky 1979).

Functional magnetic resonance imaging (fMRI) studies using the market transaction experiment suggested that the endowment effect could be attributable to brain areas related to reward or loss; such as the amygdala, insula or ventral striatum (De Martino

et al. 2009; Knutson et al. 2008; Weber et al. 2007). However, the endowment effect is known to occur instantly during the price evaluation without actual economic results (Brookshire and Coursey 1987; Hammack and Gardner 1974). It is not known whether brain regions associated with economic reward or loss will play an important role in that condition.

In order to clarify the brain representation of inconsistent value estimation induced by different frames (WTA and WTP) without any gain or loss, we investigated effects of the reference point (a virtual instant ownership) on the price evaluation using fMRI. Better understanding of virtual ownership might help us to clarify the mechanism of complex social decision-making in the real world, where people concern about personal properties. Additionally, the anatomical correlates of WTA/WTP ratio were searched by measuring the gray matter (GM) concentration using voxel-based morphometry (VBM) of the anatomical MRI (Ashburner and Friston 2005).

Subjects and Methods

Subjects.

Twenty one healthy subjects (11 females) participated in the experiment. The average age of male group (34.0 ± 4.2) was not significantly different from female group (35.0 ± 7.8). Due to uncorrectable motion artifact, functional imaging data from one subject could not be used. All were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield 1971). They had no history of any psychiatric or neurological disorders, or drug and alcohol abuse. The study protocol was approved by the Kyoto University Graduate School and Faculty of Medicine Ethics Committee. All subjects participated in the study after giving written informed consent.

Experimental paradigm

The pricing task in the present study is similar to the experimental market, but without any actual economic transactions (Fig. 1). The MRI scanning was performed for 4 sessions of 368 sec each. Each session contained 8 blocks (each lasting 24 sec) of the task under four different framings in a random order; pricing with virtual ownership (WTA: willingness to accept), pricing without virtual ownership (WTP: willingness to pay), viewing with virtual ownership (Own) and viewing without virtual ownership (View). Task blocks were preceded by a cue (8 sec) indicating the framing (WTA, WTP, Own or View) and separated by a resting period lasting 16 sec with only a central fixation point presented. One block consisted of three pricing trials with different items presented on a screen. Thus, 96 different items (24 items for each framing) were presented for each subject once in whole experiment without repetition within subjects.

The task conditions for each item were counterbalanced across subjects. This experimental procedure was to avoid the priming effect of fMRI signal change (Dehaene et al. 1998) and anchoring effect of pricing (Ariely et al. 2003), which can be caused by the repetition of the same item. If one item is repeatedly presented for one subject for different task conditions, both the brain activation and pricing behavior might be affected by their order. Photographs of all items were taken from Amazon online shop. The familiarity of items was tested on 1-5 Likert scale in a preliminary behavioral experiment, and all the items used in the fMRI experiment were scored higher than 3.

The subjects were carefully instructed in the nature of the pricing task under four different framings before the experiment. Especially, we carefully checked that the subjects understood that task is just a value estimation of items without any market transactions.

For each trial in a task block, the item was presented on the screen for 8 sec. Subjects expressed their value estimation of the item by using a non-magnetic device with three buttons, designating 100, 1000 and 10000 of the price window in the screen. Each button press changed the price value in increments of 100, 1000 or 10000, consequently. Each number started from 0 and returned to 0 if button was pressed 10 times. The expected number of button press calculated from the item's market prices was 5.1 ± 0.2 times. Therefore, in order to cancel out the motor-related brain activity, we asked subjects to press each button two (total of six) times during Own and View conditions without imaging the price in mind.

During WTA condition, the subject has to imagine that he owns the item on the screen. He is asked to indicate its price using the buttons. The price should be the lowest acceptable one for him, when he was to give up the item. During WTP condition, the subject is asked to indicate the price of the item, which should be the highest price he would pay to obtain it. For these 2 pricing tasks, the subject was told that this is not a virtual market and that the task is to make a value estimation of the item without any economic transactions.

During Own condition, the subject is asked to imagine that he owns the item on the screen. During View condition, he is asked to watch and keep attention to the items on the screen. The subjects are not demanded to make any economic evaluation during View and Own conditions but to recognize them. For Own and View conditions, the subject is instructed to press each button two (total of six) times.

Behavioral data

To normalize the difference in the prices of items, the raw price of one item determined by the subject was divided by its market price (MP) which was an actual cost of item in Amazon shop. Detailed analysis was performed using this WTA/MP or WTP/MP ratio. In the preliminary behavioral experiment in another group of subjects ($n = 7$), we confirmed that the discrepancy between WTA and WTP consistently occurred in the item set used in this study (the mean \pm SD; WTA/WTP ratio = 2.3 ± 1.0). The mean WTA price was significantly larger than the mean WTP price ($p < 0.001$).

In addition, the reaction time of the first button press was measured from the onset of the item presentation. To estimate the finger movement aspects during the task, we also analyzed the number of button press per each trial, for four conditions. The behavioral

results were statistically compared using analysis of variance (ANOVA) or t-test with the threshold at the p value of 0.05.

Image acquisition and analysis

Functional MRI

fMRI experiments were conducted on a 3T Trio whole body scanner (Siemens, Erlangen, Germany). Functional images were obtained with a T2*-weighted gradient echo, echo-planar imaging sequence. The image acquisition parameters were as follows: repetition time (TR) = 2.5s, echo time (TE) = 30ms, flip angle (FA) = 90°. For anatomical registration, we obtained high-resolution 3D T1 anatomical images after the fMRI session (magnetization prepared rapid gradient-echo sequence, 0.94x0.94x1 mm³ voxel, 2s repetition time, 4.38 ms echo time, 990 ms inversion time, 8° flip angle, 130 Hz bandwidth). Subjects lay supine on a scanner bed, with a button response device held with their right hand. They viewed visual stimuli back-projected onto a screen through a mirror. Foam pads and elastic tape were used to minimize head motion. Image analysis was performed using statistical parametric mapping software (SPM5: <http://www.fil.ion.ucl.ac.uk/spm>) on MATLAB (Mathworks Inc.) The functional images were corrected for sequential slice timing and were realigned to the first image to adjust for head movements. The realigned images were then spatially normalized to a template brain (Montreal Neurological Institute, Canada) provided with SPM5 (Ashburner et al. 1997). Finally the images were smoothed with an isotropic Gaussian Kernel of 6mm full width at half maximum.

The hemodynamic response to each block was modeled by a canonical hemodynamic

response function. The first analysis sought to investigate the brain areas associated with the value estimation using simple comparisons, such as WTA vs. View, WTP vs. View, Own vs. View and WTA vs. WTP. Secondly, to reveal brain areas activity that specifically reflects inconsistent value estimation, we examine the interaction term between factors of Pricing and Owning in the two-by-two factorial design ((WTA vs. Own) vs. (WTP vs. View)). The rationale for this is that the interaction term reveals the specific alteration of pricing activity induced by the virtual owning, which might not be exactly same as the simple contrast WTA vs. WTP.

We report results in a priori regions of interest (striatum, prefrontal lobes and insula) motivated by the fact that these are regions typically identified in neuroimaging studies financial gain evaluation (De Martino et al. 2009; Tom et al. 2007; Weber et al. 2007) at $p < 0.001$ uncorrected for multiple comparisons. The resulting activation maps were displayed onto the anatomically normalized mean T1 image derived from all subjects to identify the anatomical correlates of the activity.

Voxel-based morphometry (VBM)

To investigate the relationship between brain morphology and endowment effect in each individual, we did a regression analysis within general linear model framework (Wright et al. 1995). To have gray matter density volumes from each subject, individual 3D T1-weighted anatomical MRIs were first transformed by unified tissue-segmentation and spatial normalization (Ashburner and Friston 2000; Ashburner and Friston 2005) implemented in SPM5. We then smoothed the spatially normalized gray matter volumes with a 10-mm³ full width at half maximum Gaussian kernel. All 20 individual gray matter volumes were applied to multivariate regression analysis using the WTA/WTP

ratio as a covariate of interest and gender as a confounding factor. Since we report the results in a priori regions of interest motivated by our fMRI analysis, the liberal statistical threshold of $p < 0.005$ uncorrected was used.

Results

Behavioral data

The mean WTA/MP ratio (mean \pm SD) was significantly greater than the mean WTP/MP ratio (2.07 ± 0.7 vs. 1.39 ± 0.8 , $p < 0.001$, Fig. 2). Thus, endowment effects occurred with the mean WTA /WTP ratio of 1.74 ± 0.7 . The 95 % confidence limit for WTA/WTP ratio was $2.05 - 1.43$ and was significantly different than 1. The mean reaction time did not significantly differ for WTA (4033 ± 737 ms) versus WTP (3937 ± 664 ms). The mean number of button presses was 4.5 ± 0.3 for WTP and 4.4 ± 0.2 for WTA, which were not significantly different. Behavioral parameters were not significantly affected by gender.

Brain Activation

We initially performed the group-level SPM analysis reflecting the simple contrast between 2 conditions. Brain regions showing the greater activity for WTA or WTP compared to View were bilateral inferior frontal gyrus (IFG), insula, caudate, thalamus, parietal cortex (PC) and the medial frontal cortex (MFC) (Fig.3a). In contrast, there was no greater activation during View compared to WTA or WTP. In general, brain areas associated with WTA vs. View were similar to but greater than those associated with WTP vs. View. The comparison between WTA and WTP showed the greater activation at the right insula [$x=40$, $y=28$, $z=6$; $Z_{(\text{score})} = 3.58$, 240 mm^3] and IFG [$x=38$, $y=32$, $z=-14$; $Z_{(\text{score})} = 3.56$, 80 mm^3 , Brodmann Area (BA) 47] and [$x=56$, $y=30$, $z=12$; $Z_{(\text{score})} = 3.48$, 560 mm^3 , BA45], the MFC [$x=0$ $y=10$, $z=58$; $Z_{(\text{score})} = 3.31$, 216 mm^3] and [$x=-2$ $y=-2$, $z=70$; $Z_{(\text{score})} = 3.27$, 216 mm^3], and the left PC [$x=-56$, $y=-36$, $z=54$; $Z_{(\text{score})} = 3.53$,

504 mm³] (Fig.3b).

There was no significant activation during WTP compared to WTA. The comparison Own vs. View demonstrated the activation at the right MFC [$x=10, y=32, z=44$; $Z_{(score)} = 3.48, 56 \text{ mm}^3$] and PC [$x=0, y=-56, z=66$; $Z_{(score)} = 3.58, 56 \text{ mm}^3$]. There was no significant activation for the comparison View vs. Own.

To identify brain activity specifically related to the WTA/WTP difference, we used the contrast ((WTA vs. Own) vs. (WTP vs. View)), which reflects the interaction between Pricing and Ownership. In this contrast, only the right IFG [$x=38, y=32, z=-8$; $Z_{(score)} = 3.98, 216 \text{ mm}^3$] was activated (Fig. 4).

Gray matter concentration

To clarify the brain structural correlates of inconsistent value estimation, we conducted a correlation analysis between GM concentration and individual WTA/WTP ratio. We observed a positive correlation in the right IFG [$x=40, y=34, z=12$ $Z_{(score)} = 2.95, 88 \text{ mm}^3$], MFC [$x=-10, y=32, z=32$ $Z_{(score)} = 3.62, 232 \text{ mm}^3$] and posterior cingulate cortex (PCC) [$x=-6, y=-44, z=12$ $Z_{(score)} = 2.71, 56 \text{ mm}^3$] (Fig. 5).

Discussion

We found the functional relevance of IFG for the endowment effect during the price evaluation task without any gain or loss, extending previous studies using economic transaction experiments (De Martino et al. 2009; Knutson et al. 2008; Weber et al. 2007). Although in the present study subjects knew that the pricing task is not directly connected to the economic consequences, they stated significantly higher prices in the WTA than in WTP condition, which is consistent with previous behavioral studies (Brookshire and Coursey 1987; Horowitz and McConnell 2002; Knetsch 1989; Knetsch and Sinden 1984). In other words, the virtual ownership instantly altered the economic value estimation processing. Brain activation associated for WTA and WTP conditions shared the wide cortical-subcortical network. However, our study showed that only the activation in the right IFG was related to the effect of virtual ownership on pricing task, which should be a key element in producing difference in the evaluated price for WTA and WTP. These results suggest that the endowment effect in the present task might engage in the IFG. This possibility is also supported by the morphometric analysis of brain anatomy that demonstrated the significant positive correlation between the WTA/WTP ratio and the GM concentration of the right IFG.

During the WTA compared to WTP condition, there were significantly greater brain activations in the IFG, insula, MFC and PC possibly due to the difference in the framing, although subjects performed the similar price evaluation task. Since this difference would be related to the effect of virtual ownership on pricing, these regions are candidate areas for the brain representation of the endowment effect. Moreover, in the right IFG, two distinct activation clusters were observed, corresponding to Broadmann

areas (BA) 45 and 47. By exploiting the two-by-two design of the present experiment, the interaction analysis (Pricing x Ownership) was performed and demonstrated the activation only at BA47 of the right IFG.

By using VBM analysis, we found that the higher was the WTA/WTP ratio the more was the GM concentration in BA45 of the right IFG, MFC and PCC. Since the fMRI analysis also showed the functional relevance of the right IFG, the susceptibility to the endowment effect may be associated with the neuronal volume of that region. Structural difference in the right IFG may be due to the hereditary elements or the educational and cultural factors during the early stage of life. It should be also noted that the quantitative relationship between the cortical neuronal volume and the results of VBM or other structural analysis methodology is still uncertain and possibly affected by cell size, number or the degree of myelination (Ashburner and Friston 2000; Good et al. 2000; Good et al. 2001; Han et al. 2006; Jones et al. 2000; Kabani et al. 2001).

Previous studies suggested that the right IFG plays an important role in attentional control (Dehaene et al. 1998; Duncan 2001) and especially in response inhibition (Aron et al. 2004; Konishi et al. 1999; Rubia et al. 2003). A recent study showed the close link between the right IFG activation and the detection of behaviorally relevant cues (Hampshire et al. 2010). More specifically, several fMRI studies reported the activation of the IFG in association with economic decision-making (Hare et al. 2010; Hare et al. 2008; Knutson et al. 2008; Plassmann et al. 2007; Tobler et al. 2009). We found the BA45 and 47 activations distinctly in the right IFG, which may represent slightly different roles in the pricing task.

Animal and human studies have shown that the lateral orbitofrontal areas extending to BA47 is linked to the maintenance and manipulation of cognitive representations in

working memory (Owen 1998; Petrides 1994), episodic memory retrieval (Henson et al. 1999), planning of future actions (Adrian et al. 1996; Dias et al. 1996; Fincham et al. 2002; Fleck et al. 2006), and inhibition of the prepared response and redirection of the focus of attention (Nobre et al. 1999). Studies using the reward-related tasks observed the orbitofrontal activities in response to reward-predicting signals (Tanaka et al. 2004; Tremblay and Schultz 1999), in processing a combined signal of expected value and risk (Tobler et al. 2009), and in decision-making during uncertainty (Huettel et al. 2005).

With regards to anatomical connections, this area (BA 47/12) receives inputs from different sensory modalities: object-processed visual information from inferior temporal cortex (Barbas 1988; Morecraft and Van Hoesen 1993), projection from somatosensory areas and insula (Barbas 1988; Carmichael and Price 1995a; Carmichael and Price 1995b; Rolls 1999) as well from other brain structures such as amygdala, anterior cingulate cortex, premotor area and striatum (Barbas and Pandya 1989; Carmichael and Price 1995a; Cavada et al. 2000; Eblen and Graybiel 1995; Haber 2003; Ongur and Price 2000). Most of inputs mentioned above are reciprocal.

The meta-analysis of neuroimaging studies revealed a distinction between functions of medial versus lateral orbitofrontal areas in terms of its functional neuroanatomy. It is hypothesized that the former were correlated with monetary gain and that the latter were correlated with monetary loss (Kringelbach et al. 2003; Kringelbach and Rolls 2004; O'Doherty et al. 2001)

Thus, the possible functional role for the activated cluster in BA47, in current study, is likely integrating imagined reward and affects information, particularly evaluating a potential loss value, and modulating goal-directed behavior.

Regarding the functional role of BA 45, a recent fMRI reward studies showed that the IFG may serve as a general input region to the ventromedial prefrontal cortex during value computation (Hare et al. 2010). It is also reported that the activation in the right IFG is correlated with the goal value (Hare et al. 2008). Tobler et al found that the activation in the right IFG was increased with the safe reward (Tobler et al. 2009). Knutson et. al (2007, supplementary data) also observed the negative association between the bilateral IFG activation with the price ratio of Sell vs. Buy condition. In consistent with these studies, the activation observed in BA 45 cluster in our task is likely to be related to value computation.

It is possible that BA47 of the right IFG may modulate the behavior on the basis of this estimated value computed in BA45. Our findings suggest that the right IFG plays important role in inconsistent value estimation induced by virtual instant ownership.

Previous neuroimaging studies using the similar task stressed the importance of the insula for the endowment effect(Knutson et al. 2008) (De Martino et al. 2009). Knutson reported that the insular activation to preferred products during selling predicted the susceptibility to the endowment effect, which supports the idea that insular activation may be related to a loss aversion. De Martino observed the bilateral insular activity correlated only with decreasing prices during buying, which may reflect a risk prediction error signal. However, the latter mechanism is not likely in our experimental condition, because there was no actual economic outcome of the decision making. Since the insular activation is consistently seen in neuroimaging studies of pain and distress (Ogino et al. 2007), disgust (Wright et al. 2004), risk (Clark et al. 2008) (Paulus et al. 2003), uncertainty (Critchley et al. 2001) and unfair offers from human partners in

“Ultimate Game” (Sanfey et al. 2003), it is likely to be associated with emotional processing of the negative experiences (Singer et al. 2009). Giving up the possession makes subjects to see it as a potential loss and arouse a negative somatic state, which might be related to the insular activation. However, in our study, subjects were not asked to take a risk in pricing. This minimal or implicit loss anticipation in our study might be the reason why the insular activation for the contrast WTA vs. WTP failed to survive in the interaction analysis. Because of the task difference, it would be difficult to directly compare the present findings and the previous studies of Knutson et al. (2008) and De Martino et al. (2009).

Previous neuroimaging studies on the endowment effect suggested the functional relevance of the amygdala (Weber et al. 2007) and ventral striatum (De Martino et al. 2009; Knutson et al. 2007). However, we could not find the amygdala activation in the present study. This divergence may be due to the difference in the experimental paradigm. The study by Weber et al. (2007) compared the selling and buying price evaluation with real economic consequences. Moreover, subjects were asked to choose highly emotional MP3-songs, whereas the price evaluation task in our study was without any gain or loss. In addition, the items used in the present study were not emotionally relevant ones. It is possible that the amygdala activation in the previous study is related to the processing and recognition of the negative emotion such as fear (Critchley et al. 2002; Ogino et al. 2007) or regret (Coricelli et al. 2005) which might be linked to the possible economic loss. However, the exact role of amygdala in emotional processing is still debated (Adolphs 2008).

We did not find any significant activation of the ventral striatum, either. Recent studies in economical decision-making consistently showed the importance of the ventral striatum for the computation of anticipated gains or expected values (Knutson et al. 2007; Tobler et al. 2007; Yacubian et al. 2006). The absence of the ventral striatal activation in our study might be due to the pricing task that we employed. We carefully avoided that subjects would anticipate the possible economic consequences.

Regarding the role of MFC, one possible hypothesis is that the MFC activation may be related to the negative affective emotion induced by the imagined loss of the possessed item. Previous study showed the significant correlation between behavioral loss aversion and the brain activation of the MFC (Tom et al. 2007). Additionally, Ogino et al. (2007) showed that the imagination of pain is associated with increased activity in the MFC as a part of the pain-related neural network (Ogino et al. 2007; Vogt 2005). Another possible role of the MFC in conflict monitoring (Botvinick et al. 2001) and the control of voluntary action (Lau et al. 2004). Nachev et al, reported about anatomical distinct areas in MFC that respond to either for volition or conflict (Nachev et al. 2005). The peak activated region within MFC in our task (Figure 3b) seems to be located in the pre-SMA rather than cingulate cortex. It might be related to volitional plans, as the price setting in WTA and WTP conditions was completely under subjects' control.

Another brain area where we found the activation in the WTA vs. WTP contrast was the PC. Previous monkey studies found that the activation of lateral intra-parietal (LIP) neurons were enhanced by increasing the value of all potential targets (Bendiksby and Platt 2006). Platt and Glimcher stressed the role of posterior parietal cortex in the transformation of sensory signals into motor commands (Platt and Glimcher 1999). In

other words, these findings suggest that attention and value jointly determine sensory-motor processing in LIP that attention and value linked between each other.

Difference in findings between present study and the previous studies related to WTA/WTP discrepancy may have resulted from differences in experimental design. Subjects in our experiment did not actually possess any items presented on the screen, so it should exclude the effect of emotional and sentimental attachment to the item (Ariely et al. 2005). Thus, WTA/WTP discrepancy could be explained by an “instant endowment effect”. Kahneman et al. (1990) reported that the value that an individual assigns to different objects appears to increase as soon as that individual is given the object. Subjects demonstrated an instant endowment effect in our task even during imagination of ownership. It is reported that the reluctance to sell is higher than that to buy, suggesting that the endowment effect is essentially a problem of WTA (Kahneman et al. 1990). This behavioral observation fits with our imaging results showing the greater brain activation during WTA compared to WTP.

Reference

- Adolphs R. 2008. Fear, faces, and the human amygdala. *Current Opinion in Neurobiology* 18(2):166-172.
- Adrian MO, Julien D, Michael P, Alan CE. 1996. Planning and Spatial Working Memory: a Positron Emission Tomography Study in Humans. *European Journal of Neuroscience* 8(2):353-364.
- Ariely D, Huber J, Wertenbroch K. 2005. When Do Losses Loom Larger Than Gains? *Journal of Marketing Research* 42 (2) 134-138.
- Ariely D, Loewenstein G, Prelec D. 2003. Coherent Arbitrariness: Stable Demand Curves Without Stable Preferences*. *Quarterly Journal of Economics* 118(1):73.
- Aron AR, Robbins TW, Poldrack RA. 2004. Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences* 8(4):170-177.
- Ashburner J, Friston KJ. 2000. Voxel-Based Morphometry—The Methods *NeuroImage* 11(6):805-821
- Ashburner J, Friston KJ. 2005. Unified segmentation. *Neuroimage* 26(3):839-851.
- Ashburner J, Neelin P, Collins DL, Evans A, Friston K. 1997. Incorporating Prior Knowledge into Image Registration. *Neuroimage* 6(4):344-352.
- Barbas H. 1988. Anatomic organization of basoventral and mediodorsal visual recipient prefrontal regions in the rhesus monkey. *J comp Neurol* 276:313-342.
- Barbas H, Pandya DN. 1989. Architecture and intrinsic connections of the prefrontal cortex in the rhesus monkey. *J comp Neurol* 286:353-375.
- Bateman I, Munro A, Rhodes B, Starmer C, Sugden R. 2006. A Test of the Theory of Reference-Dependent Preferences*. *Quarterly Journal of Economics* 112(2):479-505.
- Bendiksy MS, Platt ML. 2006. Neural correlates of reward and attention in macaque area LIP. *Neuropsychologia* 44(12):2411-2420.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD. 2001. Conflict Monitoring and Cognitive Control. *Psychological Review* 108(3):624-652.
- Brookshire DS, Coursey DL. 1987. Measuring the Value of a Public Good: An Empirical Comparison of Elicitation Procedures. *American Economic Review* 77:554-566.
- Carmichael ST, Price JL. 1995a. Limbic connections of the orbital and medial prefrontal cortex in macaque monkeys. *J comp Neurol* 363:615-641.
- Carmichael ST, Price JL. 1995b. Sensory and premotor connections of the orbital and medial prefrontal cortex of macaque monkeys. *J comp Neurol* 363:642-664.
- Cavada C, Company T, Tejedor J, Cruz-Rizzolo RJ, Reinoso-Suarez F. 2000. The

- Anatomical Connections of the Macaque Monkey Orbitofrontal Cortex. A Review. *Cerebral Cortex* 10(3):220-242.
- Clark L, Bechara A, Damasio H, Aitken MRF, Sahakian BJ, Robbins TW. 2008. Differential effects of insular and ventromedial prefrontal cortex lesions on risky decision-making. *Brain* 131(5):1311-1322.
- Coase RH. 1960. The Problem of Social Cost. *Journal of Law and Economics* 3:1-44.
- Coricelli G, Critchley HD, Joffily M, O'Doherty JP, Sirigu A, Dolan RJ. 2005. Regret and its avoidance: a neuroimaging study of choice behavior. *Nat Neurosci* 8(9):1255-1262.
- Critchley HD, Mathias CJ, Dolan RJ. 2001. Neural Activity in the Human Brain Relating to Uncertainty and Arousal during Anticipation. *Neuron* 29(2):537-545.
- Critchley HD, Mathias CJ, Dolan RJ. 2002. Fear Conditioning in Humans: The Influence of Awareness and Autonomic Arousal on Functional Neuroanatomy. *Neuron* 33(4):653-663.
- De Martino B, Kumaran D, Holt B, Dolan RJ. 2009. The neurobiology of reference-dependent value computation. *J Neurosci* 29(12):3833-3842.
- Dehaene S, Kerszberg M, Changeux J-P. 1998. A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences of the United States of America* 95(24):14529-14534.
- Dias R, Robbins TW, Roberts AC. 1996. Dissociation in prefrontal cortex of affective and attentional shifts. *Nature* 380(6569):69-72.
- Duncan J. 2001. An adaptive coding model of neural function in prefrontal cortex. *Nature Reviews Neuroscience* 2(11):820-829.
- Eblen F, Graybiel AM. 1995. Highly restricted origin of prefrontal cortical inputs to striosomes in the macaque monkey. *J Neurosci* 15:5999-6013.
- Fincham JM, Carter CS, van Veen V, Stenger VA, Anderson JR. 2002. Neural mechanisms of planning: A computational analysis using event-related fMRI. *Proceedings of the National Academy of Sciences of the United States of America* 99(5):3346-3351.
- Fleck MS, Daselaar SM, Dobbins IG, Cabeza R. 2006. Role of Prefrontal and Anterior Cingulate Regions in Decision-Making Processes Shared by Memory and Nonmemory Tasks. *Cerebral Cortex* 16(11):1623-1630.
- Good C, Johnsrude I, Ashburner J, Friston K, Frackowiak R. 2000. Voxel based morphometry of 465 normal adult human brains. *Neuroimage* 11(5, Supplement 1):S607-S607.
- Good CD, Johnsrude I, Ashburner J, Henson RNA, Friston KJ, Frackowiak RSJ. 2001.

- Cerebral Asymmetry and the Effects of Sex and Handedness on Brain Structure: A Voxel-Based Morphometric Analysis of 465 Normal Adult Human Brains. *Neuroimage* 14(3):685-700.
- Haber SN. 2003. The primate basal ganglia: parallel and integrative networks. *Journal of Chemical Neuroanatomy* 26(4):317-330.
- Hammack J, Gardner B. 1974. *Waterfowl and Wetlands: Toward Bioeconomic Analysis*. Johns Hopkins University Press:95.
- Hampshire A, Chamberlain SR, Monti MM, Duncan J, Owen AM. 2010. The role of the right inferior frontal gyrus: inhibition and attentional control. *Neuroimage* 50(3):1313-1319.
- Han X, Jovicich J, Salat D, van der Kouwe A, Quinn B, Czanner S, Busa E, Pacheco J, Albert M, Killiany R, Maguire P, Rosas D, Makris N, Dale A, Dickerson B, Fischl B. 2006. Reliability of MRI-derived measurements of human cerebral cortical thickness: the effects of field strength, scanner upgrade and manufacturer. *Neuroimage* 32(1):180-194.
- Hare TA, Camerer CF, Knoepfle DT, O'Doherty JP, Rangel A. 2010. Value Computations in Ventral Medial Prefrontal Cortex during Charitable Decision Making Incorporate Input from Regions Involved in Social Cognition. *Journal of Neuroscience* 30(2):583-590.
- Hare TA, O'Doherty J, Camerer CF, Schultz W, Rangel A. 2008. Dissociating the Role of the Orbitofrontal Cortex and the Striatum in the Computation of Goal Values and Prediction Errors. *Journal of Neuroscience* 28(22):5623-5630.
- Henson RNA, Shallice T, Dolan RJ. 1999. Right prefrontal cortex and episodic memory retrieval: a functional MRI test of the monitoring hypothesis. *Brain* 122(7):1367-1381.
- Horowitz JK, McConnell KE. 2002. A Review of WTA/WTP Studies. *Journal of Environmental Economics and Management* 44(3):426-447.
- Huettel SA, Song AW, McCarthy G. 2005. Decisions under Uncertainty: Probabilistic Context Influences Activation of Prefrontal and Parietal Cortices. *Journal of Neuroscience* 3304.
- Jones SE, Buchbinder BR, Aharon I. 2000. Three-dimensional mapping of cortical thickness using Laplace's equation. *Hum Brain Mapp* 11(1):12-32.
- Kabani N, Le Goualher G, MacDonald D, Evans AC. 2001. Measurement of Cortical Thickness Using an Automated 3-D Algorithm: A Validation Study. *Neuroimage* 13(2):375-380.
- Kahneman D, Knetsch JL, Thaler RH. 1990. Experimental Tests of the Endowment

- Effect and the Coase Theorem. *The Journal of Political Economy* 98(6):1325-1348.
- Kahneman D, Knetsch JL, Thaler RH. 1991. Anomalies: The Endowment Effect, Loss Aversion, and Status Quo Bias. *The Journal of Economic Perspectives* 5(1):193-206.
- Kahneman D, Tversky A. 1979. Prospect Theory: An Analysis of Decision under Risk. *Econometrica* 47(2):263-291.
- Kahneman D, Tversky A. 1984. Choices, values, and frames. *American Psychologist* 39(4):341-350.
- Knetsch JL. 1989. The Endowment Effect and Evidence of Nonreversible Indifference Curves. *The American Economic Review* 79(5):1277-1284.
- Knetsch JL, Sinden JA. 1984. Willingness to Pay and Compensation Demanded: Experimental Evidence of an Unexpected Disparity in Measures of Value. *The Quarterly Journal of Economics* 99(3):507-521.
- Knutson B, Rick S, Wimmer GE, Prelec D, Loewenstein G. 2007. Neural predictors of purchases. *Neuron* 53(1):147-156.
- Knutson B, Wimmer GE, Rick S, Hollon NG, Prelec D, Loewenstein G. 2008. Neural antecedents of the endowment effect. *Neuron* 58(5):814-822.
- Konishi S, Nakajima K, Uchida I, Kikyo H, Kameyama M, Miyashita Y. 1999. Common inhibitory mechanism in human inferior prefrontal cortex revealed by event-related functional MRI. *Brain* 122(5):981-991.
- Kringelbach ML, O'Doherty J, Rolls ET, Andrews C. 2003. Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cereb Cortex* 13:1064-1071.
- Kringelbach ML, Rolls ET. 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Prog Neurobiol* 72:341-372.
- Lau HC, Rogers RD, Ramnani N, Passingham RE. 2004. Willed action and attention to the selection of action. *Neuroimage* 21(4):1407-1415.
- Morecraft RJ, Van Hoesen GW. 1993. Frontal granular cortex input to the cingulate (M3), supplementary (M2) and primary (M1) motor cortices in the rhesus monkey. *J comp Neurol* 337:669-689.
- Nachev P, Rees G, Parton A, Kennard C, Husain M. 2005. Volition and Conflict in Human Medial Frontal Cortex. *Current Biology* 15(2):122-128.
- Nobre AC, Coull JT, Frith CD, Mesulam MM. 1999. Orbitofrontal cortex is activated during breaches of expectation in tasks of visual attention. *Nature Neurosci*

- 2:11-12.
- O'Doherty J, Kringelbach ML, Rolls ET, Hornak J, Andrews C. 2001. Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature Neurosci* 4:95-102.
- Ogino Y, Nemoto H, Inui K, Saito S, Kakigi R, Goto F. 2007. Inner Experience of Pain: Imagination of Pain While Viewing Images Showing Painful Events Forms Subjective Pain Representation in Human Brain. *Cerebral Cortex* 17(5):1139-1146.
- Oldfield RC. 1971. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9(1):97-113.
- Ongur D, Price JL. 2000. The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cereb Cortex* 10:206-219.
- Owen A. 1998. Working memory in dorsolateral frontal cortex. *Trends in Cognitive Sciences* 2(7):239-239.
- Paulus MP, Rogalsky C, Simmons A, Feinstein JS, Stein MB. 2003. Increased activation in the right insula during risk-taking decision making is related to harm avoidance and neuroticism. *Neuroimage* 19(4):1439-1448.
- Petrides M. 1994. Frontal lobes and behaviour. *Current Opinion in Neurobiology* 4(2):207-211.
- Plassmann H, O'Doherty J, Rangel A. 2007. Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. *J Neurosci* 27(37):9984-9988.
- Platt ML, Glimcher PW. 1999. Neural correlates of decision variables in parietal cortex. *Nature* 400(6741):233-238.
- Rolls ET. 1999. *The Brain and Emotion*.
- Rubia K, Smith AB, Brammer MJ, Taylor E. 2003. Right inferior prefrontal cortex mediates response inhibition while mesial prefrontal cortex is responsible for error detection. *Neuroimage* 20(1):351-358.
- Sanfey AG, Rilling JK, Aronson JA, Nystrom LE, Cohen JD. 2003. The Neural Basis of Economic Decision-Making in the Ultimatum Game. *Science* 300(5626):1755-1758.
- Simon HA. 1955. A behavioral model of rational choice. *The Quarterly Journal of Economics* 69:99-118.
- Singer T, Critchley HD, Preuschoff K. 2009. A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Sciences* 13(8):334-340.
- Tanaka SC, Doya K, Okada G, Ueda K, Okamoto Y, Yamawaki S. 2004. Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops.

- Nat Neurosci 7(8):887-893.
- Thaler RH. 1980. Toward a positive theory of consumer choice. *Journal of Economic Behavior & Organization* 1(1):39-60.
- Tobler PN, Christopoulos GI, O'Doherty JP, Dolan RJ, Schultz W. 2009. Risk-dependent reward value signal in human prefrontal cortex. *Proceedings of the National Academy of Sciences* 106(17):7185-7190.
- Tobler PN, Fletcher PC, Bullmore ET, Schultz W. 2007. Learning-Related Human Brain Activations Reflecting Individual Finances. *Neuron* 54(1):167-175.
- Tom SM, Fox CR, Trepel C, Poldrack RA. 2007. The neural basis of loss aversion in decision-making under risk. *Science* 315(5811):515-518.
- Tremblay L, Schultz W. 1999. Relative reward preference in primate orbitofrontal cortex. *Nature* 398:704-708.
- Vogt BA. 2005. Pain and emotion interactions in subregions of the cingulate gyrus. *Nat Rev Neurosci* 6(7):533-544.
- Weber B, Aholt A, Neuhaus C, Trautner P, Elger CE, Teichert T. 2007. Neural evidence for Reference-dependence in real-market-transactions. *Neuroimage* 35(1):441-447.
- Wright IC, McGuire PK, Poline JB, Travers JM, Murray RM, Frith CD, Frackowiak RSJ, Friston KJ. 1995. A Voxel-Based Method for the Statistical Analysis of Gray and White Matter Density Applied to Schizophrenia. *Neuroimage* 2(4):244-252.
- Wright P, He G, Shapira NA, Goodman WK, Liu Y. 2004. Disgust and the insula: fMRI responses to pictures of mutilation and contamination. *Neuroreport* 15(15):2347-2351.
- Yacubian J, Glascher J, Schroeder K, Sommer T, Braus DF, Buchel C. 2006. Dissociable Systems for Gain- and Loss-Related Value Predictions and Errors of Prediction in the Human Brain. *Journal of Neuroscience* 26(37):9530-9537.

Figure Legends

Figure 1

Schema of the one block of the experimental task. Subjects participated in the 4 sessions, where each session contained 8 blocks of the task under four different conditions in a random order; pricing with virtual ownership (WTA), pricing without virtual ownership (WTP), viewing with virtual ownership (Own) and viewing without virtual ownership (View). One block consisted of three pricing trials with different items presented on a screen, preceded by a cue which indicates the condition. Subjects during pricing period should judge its price and indicate it on the screen, using 3 buttons device, and then fixated on a cross point (16 s) prior to the onset of the next trial.

Figure 2.

Price ratios (mean \pm SD) for the WTA/market price (MP), WTP/MP and WTA/WTP. WTA/MP was significantly larger than WTP/MP ($p < 0.001$).

Figure 3.

(a) Activation related to pricing. (WTA vs. View) and (WTP vs. View) contrasts are superimposed on the coronal slices of MRI, indicated as red and green pixels, respectively. Consequently, yellow pixels indicate the superimposed image of both contrasts. In this and other activation maps, the statistical threshold is set at $p < 0.001$ uncorrected. Brain activation for WTA mostly include that for WTP and is widely observed in MFC, bilateral IFG, insula, thalamus and PC.

(b) Activation related to the contrast WTA vs. WTP. The greater activation for WTA compared to WTP is shown at the right IFG (cluster 1: BA 47, cluster 2: BA 45), insula,

MFC and the left PC.

Figure 4.

Activation related to WTA/WTP disparity. Significant BOLD signal change of the right IFG is illustrated for interaction analysis between Pricing and Ownership ((WTA vs. Own) vs. (WTP vs. View)). This activated region is close to cluster 1 in Fig.3b

Figure 5.

Statistical parametric map of GM concentration by regression analysis with WTA/WTP ratio. Positive correlation is observed at the right IFG and MFC. It is close to cluster 2 in Fig.3b









